

The decoupled nature of basal metabolic rate and body temperature in endotherm evolution

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1 *Title:* The decoupled nature of basal metabolic rate and body temperature in endotherms
2 evolution

3

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22 The origin of endothermy in birds and mammals are iconic events in vertebrate
23 evolution. Endotherms can maintain their body temperature (T_b) over a wide range
24 of ambient temperatures (T_a) using primarily the heat generated continuously by
25 their high basal metabolic rates (BMR)¹. There is also an important positive
26 feedback loop in that BMR itself is influenced by T_b ¹⁻³. Owing to this, many
27 ecologists and evolutionary physiologists posit that the evolution of BMR and T_b
28 must have been coupled during the radiation of endotherms³⁻⁵, changing with
29 similar trends⁶⁻⁸. However, colder historical environments might have imposed
30 strong selective pressures on BMR to compensate for increased rates of heat loss and
31 to keep T_b constant⁹⁻¹². Thus, adaptation to cold T_a via BMR increases could have
32 decoupled BMR from T_b and caused different evolutionary routes to the modern
33 diversity in these traits. Here we show that BMR and T_b were decoupled in ~ 90% of
34 mammalian and in ~ 36 % of avian phylogenetic branches. Mammalian BMR
35 evolved with rapid bursts but without any long-term directional trend, whereas T_b
36 evolved mostly at a constant rate and towards colder bodies from a warmer-bodied
37 ancestor. Avian BMR evolved predominantly at a constant rate – again with no
38 trend, whereas T_b evolved with much greater rate heterogeneity than BMR and
39 there has been adaptive evolution towards colder bodies. Furthermore, rapid shifts
40 leading to both BMR increases and decreases were linked to abrupt changes
41 towards colder T_a but only in mammals. Our results suggest that natural selection
42 effectively exploited the diversity of mammalian BMR under diverse, often adverse
43 historical thermal environments.

45 Phylogenetic statistical methods^{13, 14} now provide us with the opportunity to formally test
46 whether BMR has been linked to T_b or T_a throughout the evolution of birds and mammals.
47 By accommodating for and identifying heterogeneity in the rate of phenotypic evolution
48 these methods can detect and reconstruct accurate historical evolutionary processes¹⁵.
49 Evaluation of the evolutionary coupling between BMR and T_b has direct consequences for
50 several longstanding ecological and evolutionary theories (including the Metabolic
51 Theory of Ecology) which assume coupling²⁻⁸.

52
53 We first quantified and compared rates for BMR and T_b evolution along each branch of
54 the time-calibrated phylogenetic trees of birds and mammals (henceforth *branch-wise*
55 *rates*, r ; see Methods). r measures how fast a trait evolved along an individual

phylogenetic branch (r is a rate scalar by which the background rate is multiplied to increase or decrease the pace of evolution). If BMR and T_b were coupled during the evolution of endotherms, the amount of change along phylogenetic branches in both traits should be positively associated – where r is high in BMR we expect it to be high in T_b (Fig. 1 b). We tested this prediction against alternative evolutionary scenarios. Firstly, we cannot make any inferences about coupling or decoupling where there is no rate heterogeneity for both BMR and T_b ($r = 1$ for all branches in the tree for both traits; Fig. 1a). Secondly, we infer decoupled evolution if both traits show rate heterogeneity, but the magnitudes of r s are negatively correlated (*i.e.* branches evolving at a high rate for BMR are evolving at a low rate for T_b , and vice-versa, Fig. 1c). We suggest this scenario implies decoupled evolution because a negative correlation most likely implies that one trait tends to be conserved whilst the other evolved rapidly. Thirdly, we infer decoupled evolution if only one trait shows rate heterogeneity while the other evolved at a constant rate (Fig 1d and e) or if both traits show heterogeneity but the *branch-wise rates* are not associated (Fig 1f).

As BMR , body mass ($Mass$), T_b , and T_a are at least to some extent correlated in extant birds and mammals, and such correlations may vary between orders¹⁶, we estimated the *branch-wise rates* for BMR and T_b while accounting for their covariates across extant species using the *phylogenetic variable-rates regression* model¹⁷ (henceforth *variable-rates*; Methods). This approach allows for simultaneous estimation of both an overall relationship between, for instance, BMR as a function of $Mass$ and T_b across extant species, and any shifts in rates (r) that apply to the phylogenetically structured residual

variance in the relationship. In both birds and mammals, the *variable-rates* model significantly fits the data better than the *constant-rate regressions*, which assume a single rate across all branches (Methods; Table S1 to S8). The best fitting *variable-rates* model for mammalian *BMR* includes both *Mass* and T_b with a single slope for each trait estimated across all orders (Table S1 and S2). For mammalian T_b , the best fitted model includes *Mass* and *BMR* as covariates, also with a single slope across all orders (Table S3 and S7). In birds, the best model for *BMR* includes only *Mass* with a single slope for all orders (Table S4). Finally, the best fitted model for avian T_b includes *Mass* only in Columbiformes (Table S6).

The *branch-wise rates* estimated in the best fitting models shows that mammalian *BMR* evolved at a constant rate ($r = 1$) in just 11.2% of branches and at faster rates ($r > 1$) in 88.8% of branches (Fig. 2a). Mammalian T_b evolved at a constant rate in 70.3% of branches and faster rates in 29.7% of branches (Fig. 2b). In birds, *BMR* evolved at a constant rate in 90.5% of branches and at faster rates in 9.5% of branches (Fig. 2d). Avian T_b evolved at a constant rate in 69 % of branches and at faster rates in 31% (Fig. 2e). When the *branch-wise rates* for *BMR* and T_b were compared, we found that in mammals, both traits evolved at a constant rate in 10.6% of branches (Fig. 3a consistent with Fig. 1a). In 60.2% of branches only one trait evolved at faster rates while the other trait diverged at a constant rate. This indicates that *BMR* and T_b evolved in a decoupled fashion along these branches (Fig. 3a consistent with Fig. 1d, e). We found that 29.2% of branches had an increased rate in both *BMR* and T_b . However, the magnitudes of the *branch-wise rates* were not significantly correlated (p_{MCMC} [% of posterior distribution

crossing zero] = 9%; Table S9; Fig. 3a consistent with Fig 1f). This also suggests decoupled evolution in those branches – likely because of distinct selection pressures acting on *BMR* and T_b . On the other hand, both traits evolved at a constant rate in 63.8% of branches for birds (Fig. 3c consistent with Fig. 1a). In 32% of branches only one trait evolved at fast rates while the other trait diverged at a constant rate (Fig. 3c consistent with Fig. 1d, e). In the remaining 4.2% of branches, both traits evolved at faster rates, but the r magnitudes were not statistically correlated ($p_{\text{MCMC}} = 16.9\%$, Table S10, Fig. 3c consistent with Fig. 1f).

As rapid bursts in *BMR* evolution were not coupled with those in T_b evolution, we evaluated the alternative hypothesis postulating that *BMR* evolved in response to T_a . This hypothesis suggests that colder environments increase the rate of heat lost from organisms which is subsequently compensated by *BMR* increases⁹⁻¹². These *BMR* increases could have occurred over long periods of time because of global cooling¹⁸ - generating a long-term directional trend in *BMR* during the radiation of mammals and birds. This expectation is in line with the Plesiomorphic-Apomorphic Endothermy Model⁶⁻⁸ (PAE Model). By assuming that *BMR* and T_b are coupled in endotherms and that they both can be used as a proxy of the degree of endothermy, the PAE model predicts a general tendency towards higher endothermic levels through time (from basoendothermic ancestors, Methods) associated with the Cenozoic global cooling. Global cooling is not the only source of variation in T_a . Long-term directional increases in *BMR* might have also been driven by historical dispersals of endotherms towards higher latitudes¹⁹. In either case, if a long-term decrease in T_a drove adaptation via *BMR* elevation, and T_b

125 followed the same trajectory (as assumed by the PAE model) we expect to find a positive
126 correlation between the *branch-wise rates* of *BMR* and the *branch-wise rates* of T_a . With
127 this in mind, we also expect a positive trend towards higher *BMR* and T_b values from
128 basoendothermic ancestors and a negative trend towards lower T_a from warmer ancestral
129 environments. We used the *variable-rates* model to estimate the *branch-wise rates* for T_a
130 whilst accounting for latitude since, generally, T_a decreases from the equator to the poles
131 (Methods; Table S11).

132
133 The *variable-rates* model significantly improved the fit to the T_a data over the *constant-*
134 *rate* regression model in both mammals and birds (Table S11). In 21.2% of mammalian
135 branches T_a evolved at a constant rate, and with rate heterogeneity in the remaining
136 78.8% – including 72.2% of branches with faster rates and 6.6% with slower rates ($r < 1$,
137 Fig. 2c). This indicates that most ancestral mammalian lineages (72.2%) faced abrupt
138 historical changes in their T_a , while far fewer lineages (6.6%, mostly bats) survived and
139 continued existing in similar thermal environments. In birds, 77.6% of branches show
140 faster rates of T_a change, 22.1% show changes at a constant rate, and in only a single
141 branch the T_a changed at a slower rate (Fig. 2f).

142
143 When *branch-wise rates* of mammalian *BMR* and T_a evolution were compared, we found
144 that they were coupled in 74.9% of branches ($p_{\text{MCMC}} = 0\%$; Table S12; Fig. 3b, consistent
145 with Fig. 1b). To evaluate further if T_a decreases were linked to *BMR* increases in the
146 74.9% of mammals where both traits were coupled (i.e. to ascertain the direction of
147 change), we evaluated the expected positive trend in *BMR* as a response to the long-term

decrease in T_a . We conducted Bayesian phylogenetic regressions between extant values of these two variables (in turn) and the *path-wise rates* (sum of *branch-wise rates* along branches in the path from the root of the tree to each terminal species, Methods)¹⁵. We found a negative effect of *path-wise rates* on T_a across all mammals (Fig. 4b; Table S14), which supports a long-term directional trend towards habitats with lower T_a over time. However, we did not find evidence for any trend in mammalian *BMR* evolution – *BMR* increases and decreases were equally likely in our sample (Table S14). Our results suggest that in colder environments, where resources were available to fuel metabolic elevation, selection favoured higher mammalian *BMR*²⁰. Another possibility might be that *BMR* increase was a correlated response to direct selection on other physiological traits, like maximal metabolic capacities for thermogenesis, whose benefits outweigh the energetic cost of *BMR* elevation²⁰. Otherwise, selection may have always favoured *BMR* decreases under an ever colder environment²⁰.

In contrast to mammals, most avian branches that experienced rapid shifts in T_a did not show evidence of coupled changes in *BMR* – 68.4% of branches had fast rates of T_a evolution but a constant rate of *BMR* evolution (Fig. 3d consistent with Fig. 1d, e). Moreover, the small fraction of branches where *BMR* evolved at fast rates (9.5%) were not linked to rapid shifts in T_a (Fig. 3d consistent with Fig. 1f; Table S13). Avian *BMR* did not show a positive evolutionary trend despite the fact they also experienced colder environments over time (Fig. 4d; Table S15). Birds might not have responded to colder temperatures by changes in their *BMR* because their lower thermal conductance might

have helped them retain internal heat⁹. Alternatively, other physiological strategies, such as torpor, may have been selected for under colder environments²¹.

Finally, we found a negative effect of *path-wise rates* on T_b in both mammals (Fig. 4a; Table S14) and birds (Fig. 4c; Table S15). This suggest that – on average – endotherms evolved towards colder bodies from warmer-bodied ancestors. These directional models predict a mean T_b of 35.3 °C and 40.4 °C in the most recent common ancestor (MRCA) of mammals and birds respectively (Fig. 4a, c), suggesting that early birds and mammals were mesoendotherm rather than basoendotherms (Methods). This result does not support that ancestral mammals could not attain $T_b > 30$ °C owing to the elevated metabolic rates necessary to compensate heat loss in cold environments²². However, if the $T_b - T_a$ differential (ΔT) determines how hot early mammals were, we expect that the mammalian MRCA with a T_b of 35.3 °C could survive in an environment warm enough to have a low ΔT . Our model describing the negative trend in T_a predicts that the MRCA of mammals lived in an environment with 23 °C on average (Fig. 4b), resulting in a ΔT of 15.3 °C. This ancestral ΔT is very conservative compared with the ΔT s observed in extant mammals. For example, there are small mammals that achieve T_b higher than 39 °C (e.g. *Microdipodops pallidus*¹⁶) that can survive in environments of 11 °C¹⁹ ($\Delta T = 28$ °C). Also, some larger mammals have stable T_b even in extreme environmental conditions – the Artic hare (*Lepus arcticus*) can maintain its T_b of 38 °C¹⁶ in temperatures as low as -12 °C¹⁹ ($\Delta T = 50$ °C).

Taken together, our results reveal that *BMR* was not coupled with T_b across the evolution of endothermic species. As environments became colder, mammals survived by changing their *BMR*, while birds likely survived owing to their high thermal insulation. Evaluating the isolated and/or combined effect of environmental variables on physiological attributes has implications for evidence-based projections for the future²³. In this sense, the previously unappreciated complexity, interplay and decoupled nature in the evolutionary history of *BMR*, T_b and T_a might point to undetected resilience of endotherms in the face of modern global challenges.

Figure legends.

Figure 1. Possible evolutionary scenarios between *BMR* and T_b given their branch-wise rates (r) in a bivariate space. Grey colours represent the constant background rate ($r = 1$). Red colours represent rates faster than the background rate ($r > 1$) and blue colours represent rates slower than the background rate ($r < 1$), which might be related to past events of positive¹⁷ and stabilizing selection²⁹ respectively. Point fill colours represent *BMR* rates and point outline colours represent T_b rates.

Figure 2. Branch-wise rates (r) of *BMR*, T_b , and T_a on the mammalian and avian phylogeny. Silhouettes courtesy of Phylopic/Apokryltaros (vectorized by T. Michael Keeseey), Becky Barnes, Doug Backlund et al., Emily Willoughby, Enoch Joseph et al., Estelle Bourdon, Ferran Sayol, FunkMonk, Jon Hill (Photo by DickDaniels), L. Shyamal, Lip Kee Yap (modified), Mathew Callaghan, Matt Martyniuk, nicubunu, Pearson Scott

Foresman, Prin Pattawaro et al., Rebecca Groom, Sarah Werning, T. Michael Keeseey

(after Joseph Wolf), Yan Wong, Steven Traver. Silhouette licence links:

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Figure 3. Branch-wise rates (r) of BMR , T_b , and T_a in bivariate space for mammals

(a, b) and birds (c, d). Bayesian GLS analyses indicates that only fast *branch-wise rates* for BMR and slow-fast *branch-wise rates* of T_a were statistically correlated in mammals ($p_{MCMC} = 0$; $n = 602$ branches; black line).

Figure 4. Mammals (a, b) and birds (c, d) evolved towards both colder T_b and T_a

over their evolutionary history. *Path-wise rates* had a significant negative effect in mammalian and avian T_b ($p_{MCMC} = 4\%$ and 3% ; $n = 502$ and 367 species) and in mammalian and avian T_a ($p_{MCMC} = 0$ and 0 ; $n = 2922$ and 6142 species), both supporting a negative macroevolutionary trend¹⁵. Transparent and dark lines indicate the posterior distribution of slopes and the mean slope respectively, estimated from the Bayesian PGLS (Methods).

Methods.

Data. We used a time-calibrated phylogenetic tree of extant mammals ($n = 3321$)²⁴, and the body mass (M), basal metabolic rate (BMR), and body temperature (T_b) taken from Clarke et al.¹⁶ ($n = 632$). After identifying species in the tree that have trait information,

we obtained a final mammalian dataset of 502 species, which includes representatives from 15 orders (SI).

For birds, we used the consensus time-calibrated tree from Rolland et al.¹⁹. This tree was inferred from the samples of trees provided by Jetz et al.²⁵. Data for *BMR*, T_b , and *Mass* were obtained from Fristoe et al.⁹. After matching this database with the phylogenetic tree, we obtained a final sample of 164 species which includes representatives from 21 orders (SI). The dataset used to evaluate evolutionary trends in T_b (see below) is from Clarke & Rothery²⁶, which contains 367 species with phylogenetic information.

Data for ambient temperature (T_a) and latitude for extant mammals and birds was extracted from Rolland et al.¹⁹. These datasets include 2922 species of mammals and 6142 species of birds which have phylogenetic information. The T_a for extant endothermic species is the temperature of environments in which birds and mammals inhabit today – measured as the mean ambient temperature for the mid-point latitude of each species distribution (Rolland et al.¹⁹). The T_a at which a species exists today may not be a heritable trait *per se*. However, the evolution of T_a can still be inferred using phylogenetic methods since habitat selection reflects species adaptations (traits) to some characteristics of the environment. This interrelationship should leave phylogenetic signal in the T_a at which endothermic species live. Accordingly, we found significant phylogenetic signal in the T_a of both mammals ($\lambda_{\text{PosteriorMean}} = 0.77$; Bayes Factor = 665) and birds ($\lambda_{\text{PosteriorMean}} = 0.8$; Bayes Factor = 1404). Furthermore, the phylogenetic signal for T_a is very high ($\lambda=1$) in birds and mammals, when estimated using the median- r scaled tree.

260

261 Finally, to evaluate the endothermic levels for the MRCA of mammals and birds
262 proposed by Lovegrove^{7, 8}, we followed his categorization of endothermic species as
263 basoendotherms ($T_b^{\text{Birds}} < 40.4\text{ °C}$; $T_b^{\text{Mammals}} < 35.0\text{ °C}$), mesoendotherma ($40.4\text{ °C} \leq$
264 $T_b^{\text{Birds}} \leq 42.5\text{ °C}$; $35\text{ °C} \leq T_b^{\text{Mammals}} \leq 37.9\text{ °C}$), and supraendotherms ($T_b^{\text{Birds}} > 42.5\text{ °C}$;
265 $T_b^{\text{Mammals}} > 37.9\text{ °C}$).

266

267 **Inferring the *branch-wise rates* of evolution.** We identified heterogeneity in the rate of
268 evolution along phylogenetic branches (*branch-wise rates*) by dividing the rate into two
269 parameters: a background rate parameter (σ_b^2) which assumes changes in the trait of
270 interest (e.g. *BMR*) are drawn from an underlying Brownian process, and a second
271 parameter, r , that identifies a branch-specific rate shift. A full set of *branch-wise rates* are
272 estimated by adjusting the lengths of each branch in a time-calibrated tree (stretching or
273 compressing a branch is equivalent to increasing or decreasing the phenotypic rate of
274 change relative to the underlying Brownian rate of evolution). *Branch-wise rates* are
275 defined by a set of branch-specific scalars r ($0 < r < \infty$) which transform each branch in
276 order to optimize the phenotypic rate of change to a Brownian process ($\sigma_b^2 r$). If
277 phenotypic change occurred at accelerated (faster) rates along a specific branch of the
278 tree, then $r > 1$ and the branch is stretched. Decelerated (slower) rates of evolution are
279 detected by $r < 1$ and the branch is compressed. If the trait evolves at a constant rate
280 along a branch, then the branch will not be modified (*i.e.* $r = 1$).

281

We estimated the r values of BMR , T_b , and T_a evolution using the *phylogenetic variable-rates regression* model in a Bayesian framework¹⁷. This model is designed to automatically detect shifts in the rate of trait evolution across phylogenetic branches while accounting for a relationship with another trait or traits across extant species values. This approach allows for simultaneous estimation of both an overall relationship between, for instance, BMR as a function of $Mass$ and T_b across extant species, and any shifts in rates (r) that apply to the phylogenetically structured residual variance in the relationship. As residual variance is explained by shifts in rate across phylogenetic branches we can, for example, determine how much BMR has changed in the past (r) after accounting for their covariation with $Mass$ and T_b in the present (the relationship between the values across extant species). Thus, if the amount of BMR change along individual phylogenetic branches were coupled with the amount of change of T_b , then we should find the r values of BMR to be positively associated with the r values of T_b . The *branch-wise rates* for T_b evolution can be estimated while accounting for its covariation with other traits or factor across extant species. Previous studies on the association between BMR and T_b using extant species values alone have not evaluated the association in evolutionary terms even when they use phylogenetic method.

We evaluated 24 *phylogenetic variable-rates regression models* and 24 *phylogenetic constant-rate regression models* (Table S1 to S8). Regression model selection was conducted using Bayes Factors (BF) via marginal likelihoods estimated by stepping stone sampling. BF is calculated as the double of the difference between the log marginal-likelihood of the complex model and the simple model. By convention, $BF > 2$ indicates

positive evidence for the complex model, BF 5-10 indicates strong support, and $BF > 10$ are considered very strong support²⁷. We inferred the r values of BMR and T_b with the *phylogenetic variable-rates regression models* that best fit the data for our samples of mammals and birds (Table S7 and S8). We also estimated the r values for T_a after accounting for the effect of latitude of species distribution (Table S11) and, consequently, we accounted for the geographic variation of T_a across extant species distributions. We used BayesTraits v3.0²⁸ to detect the magnitude and location of r in a Bayesian Markov chain Monte Carlo (MCMC) reversible-jump framework, which generates a posterior distribution of trees with scaled branches lengths according to the rate of evolution. There is no limit or prior expectation in the number of the r branch-scalars, r numbers vary from zero (no branch is scaled) to n , where n is the number of branches in the phylogenetic tree. Regarding the values of each r parameter, we used a gamma prior, with $\alpha = 1.1$ and β parameter rescaled in order to get the median of the distribution equal to one. With this setting, the numbers of rate increases and decreases proposed is balanced¹³. We ran 50,000,000 iterations sampling every 25,000 to ensure chain convergence and independence in model parameters in BMR and T_b analyses. We discarded the first 25,000 iterations as burn in. For the T_a analysis in mammals we ran 200,000,000 iterations sampling every 100,000, and we discarded the first 100,000 iterations as burn in. For T_a analysis in birds we ran 400,000,000 iterations discarding the first 100,000,000 as burn in, and we sampled every 200,000. Regression coefficients were judged as significant according to a calculated p_{MCMC} value for each posterior of regression coefficients: where $< 5\%$ of samples in the posterior distribution crossed zero, this indicates that the coefficient is significantly different from zero.

328

329 **Testing the relationship between the *branch-wise rates* of evolution.** We first
330 estimated the consensus branch-scaled tree for *BMR* and T_b from the posterior sample of
331 branch-scaled trees obtained with the *phylogenetic variable-rates regression model*. The
332 consensus branch-scaled tree was generated by using the median r from the posterior
333 distribution. We evaluated the correlation between the r values for *BMR* and T_b using a
334 Bayesian GLS regression in BayesTraits v3.0. The same analyses were conducted to
335 evaluate the correlation between *branch-wise rates* for *BMR* and T_a . We used a uniform
336 prior for the β (slope coefficient) ranging from -100 to 100. We ran 50,000,000 iterations
337 sampling every 25,000 to ensure chain convergence and independence in model
338 parameters. Significance of regression coefficients were determined as above.

339

340 **Detecting trends.** We evaluated the direction of change in *BMR*, T_b , and T_a across all
341 mammals and birds using the *path-wise rates* of these variables (Table S15 and S16).
342 *Path-wise rate* is the sum of all the *branch-wise rates* along the path of a species, which
343 lead from the root (the MRCA) to the tips of the tree, and it accounts for the total changes
344 the species has experienced during its evolution¹⁵. If high *path-wise rates* have
345 disproportionately been associated with trait increases or decreases, we expect to find that
346 species with greater *path-wise rates* will have high or low trait values in the present. For
347 instance, if ancestral mammals experienced progressively colder environmental
348 temperatures owing to climate change or colonization of colder habitats as they were
349 evolving from their MRCA, we expect a negative correlation between the *path-wise rate*
350 of T_a and the T_a of extant species. We performed six Bayesian PGLS regressions in

BayesTraits 3.0 to evaluate the relationship between BMR , T_b , T_a and their *path-wise* rates (Table S15 and S16). We used a uniform prior for the β (slope coefficients) ranging from -100 to 100 to allow all possible values to be equally likely. Finally, we ran 50,000,000 iterations sampling every 25,000 to ensure chain convergence and independence in model parameters. Significance of regression slopes were determined as above.

End notes.

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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374

375 **Data availability statement.** Correspondence and request for materials should be
376 addressed to J.A-LL. (jorgeavariall@gmail.com) or C.V. (c.d.venditti@reading.ac.uk).

377

378 **References**

379

380 1. Clarke, A. *Principles of Thermal Ecology. Temperature, Energy and Life.* (Oxford
381 University Press, 2017)

382

383 2. Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of
384 size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2002).

385

386 3. Clarke, A., & Pörtner H-O. Temperature, metabolic power and the evolution of
387 endothermy. *Biol. Rev.* **55**, 703-727 (2010).

388

389 4. Kemp, T. S. The origin of mammalian endothermy: a paradigm for the evolution of
390 complex biological structure. *Zool. J. L. Soc.* **147**, 473–488 (2006).

391

392 5. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Towards a
393 metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).

394

395 6. Lovegrove, B. G. The evolution of endothermy in Cenozoic mammals: a
396 plesiomorphic-apomorphic continuum. *Biol. Rev.* **87**, 128-162 (2012).

397

398 7. Lovegrove, B. G. The evolution of mammalian body temperature: the Cenozoic
399 supraendothermic pulses. *J. Comp. Physiol. B.* **182**, 579-589 (2012).

400

401 8. Lovegrove, B. G. A phenology of the evolution of endothermy in birds and mammals.
402 *Biol. Rev.* **92**, 1213-1240 (2017).

403

404 9. Fristoe, T. S. *et al.* Metabolic heat production and thermal conductance are mass-
405 independent adaptations to thermal environment in birds and mammals. *PNAS* **112**.
406 15934-15939 (2015).

407

408 10. Naya, D. E., Naya, H., White, R. C. On the interplay among ambient temperature,
409 basal metabolic rate, and body mass. *Am. Nat.* **192**, 518-524 (2018).

410

411 11. White, C. R., Blackburn, T. M., Martin G. R., Butler, P. J. Basal metabolic rate of
412 birds is associated with habitat temperature and precipitation, not primary productivity.
413 *Proc. Biol. Sci.* **274**, 287-293 (2007).

414

415 12. Jetz, W., Freckleton, R. P., McKechnie, A. E. Environment, migratory tendency,
416 phylogeny and basal metabolic rate in birds. *PLoS ONE* 3(9):e3261.
417 doi:10.1371/journal.pone.0003261 (2008).

418

13. Venditti, C., Meade, A. & Pagel, M. Multiples routes to mammalian diversity. *Nature* **479**, 393–396 (2011).
14. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* 9:e89543 (2014).
15. Baker, J., Meade, A., Pagel, M. & Venditti, C. Adaptive evolution toward larger size in mammals. *PNAS*. **112**, 5093-5098 (2015).
16. Clarke, A., Rothery, P. & Isaac, N. J. B. Scaling of basal metabolic rate with body mass and temperature in mammals. *J. Anim. Ecol.* **79**, 610-619 (2010).
17. Baker, J., Meade, A., Pagel, M. & Venditti, C. Positive phenotypic selection inferred from phylogenies. *Zool. J. Linn. Soc.* **118**, 95-115 (2016).
18. Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*. **292**, 686-693 (2001).
19. Rolland, J. *et al.* The impact of endothermy on the climatic niche evolution and the distribution of vertebrate diversity. *Nat. Ecol. Evol.* **2**, 459-464 (2018).

20. Swanson, D. L., McKechnie, A. E., Vézina, F. How low can you go? An adaptive energetic framework for interpreting basal metabolic rate variation in endotherms. *J. Comp. Physiol. B.* **187**, 1039-1056 (2017).
21. Körtner, G., Brigham, R. M. & Geiser, F. Winter torpor in a large bird. *Nature.* **407**, 318 (2000).
22. Crompton, A. W., Taylor, C. R. & Jagger, J. A. Evolution of homeothermy in mammals. *Nature* **272**, 333-336 (1978).
23. Bozinovic, F. & Pörtner, H-O. Physiological ecology meets climate change. *Ecol. Evol.* **5**, 1025–1030 (2015).
24. Fritz, S. A., Bininda-Emonds, O. R. & Purvis, A. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol Lett* **12**, 538-549 (2009).
25. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature.* **491**, 444-448.
26. Clarke, A. & Rothery, P. Scaling of body temperature in mammals and birds. *Func. Ecol.* **22**, 58–67 (2008).

- 463 27. Raftery, A.E. in *Markov Chain Monte Carlo in Practice* (eds Gilks, W. R.,
464 Richardson, S. & Spiegelhalter, D. J.) 163–187 (Chapman & Hall, 1996).
465
- 466 28. Pagel, M., Meade, A. & Barker, D. Bayesian estimation of ancestral character states
467 on phylogenies. *Systematic Biology* **53**, 673–684 (2004).
468
- 469 29. Lieberman, B. S. & Dudgeon, S. An evaluation of stabilizing selection as a
470 mechanism for stasis. *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**, 229-238
471 (1996).